

THE SYSTEMATIC POSITION OF THE JURASSIC BRACHIOPOD *CADOMELLA*

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ABSTRACT. Shell structural and morphological studies of *Cadomella* and various species of the Spiriferida and Chonetacea show that *Cadomella* belongs to the Koninckinacea within the Spiriferida. The term supra-apical is considered inappropriate for the pedicle foramen of the Koninckinacea. The relationship between pseudopunctae and tubercles is discussed.

WORKING independently (MacKinnon on the Spiriferida and Brunton on the Chonetidina) we reached the same conclusions as to the systematic position of the Koninckinacea and it seemed sensible, therefore, to combine our information into one paper. Our results show that *Cadomella* should be retained within the Koninckinacea and that this superfamily belongs to the Spiriferida. Unless otherwise stated the classification here employed follows the brachiopod 'Treatise' (Muir-Wood 1965).

During the past ten years the Lower Jurassic genus *Cadomella*, the sole member of the Cadomellacea (Muir-Wood 1955, p. 90) has received attention because of its unusual combination of morphology and shell structure; features which have resulted in its being classified within either the Strophomenida or Spiriferida. The species assigned to *Cadomella*, *C. moorei* (Davidson), the type species, *C. quenstedti* Rau and *C. davidsoni* (Eudes-Deslongchamps) were originally described as strophomenaceans.

Muir-Wood (1955) wrote of strophomenide characteristics, including a supra-apical foramen, in *Cadomella*, and in 1962, in her monograph entitled 'Chonetoidea', she included the Cadomellacea in her new classification of the Chonetidina. She wrote (1962, p. 30) that the 'Cadomellacea are dealt with elsewhere', unfortunately without actually having done so. It seems, however, that she may have thought that genera other than *Cadomella* alone were involved, for she stated that the geological range was '?Trias to Upper Lias' in the familial diagnosis. In the brachiopod Treatise Muir-Wood (1965) followed her 1962 classification, retaining the Cadomellacea in the Chonetidina, but only *Cadomella* was included and the range was limited to Lower Jurassic. The diagnosis includes mention of a functional supra-apical pedicle foramen, lack of hinge spines and a lamellar, fibrous, and internally pseudopunctate shell structure.

Boucot, Johnson, and Staton (1965), in the Treatise, placed the Triassic and Jurassic Koninckinacea within the athyrididid Spiriferida. Previously constituent genera had commonly been assigned to the Strophomenida. Cowen and Rudwick (1966) described the discovery of a spiral brachidium in *Cadomella davidsoni* from the Upper Lias of Normandy. They recognized the similarity between *Cadomella* and the Koninckinacea, but placed this superfamily within the Chonetacea. This assignment of the Koninckinacea to the Strophomenida was made in the belief that foramina were supra-apical and on the basis of morphological features such as profile, strophic hinge, and convex pseudodeltidium and notothyrium. In support of the implication that in this group a spiral brachidium must have evolved independently from that of the Spiriferida Cowen

and Rudwick (1966) quote Williams (1953) who, at that time, suggested that the spire-bearing *Thecospira* was a Triassic davidsoniacean.

Williams (1968), in his survey of articulate brachiopod shell structure, noted that the shell of *Cadomella* and *Koninckina* was identical, but not strophomenide. He described a thin primary layer followed by secondary fibres, forming an internal mosaic comparable to the standard shell structure seen in spiriferides. In addition a tertiary prismatic layer, again as in the Spiriferida, was recognized. He showed too that the shell of *Thecospira* consisted of two standard calcareous layers and reassigned both it 'and *Cadomella* and its associates to the Spiriferida' (1968, p. 48). Recently Jaanusson (1971, p. 44), in his study of brachiopod articulation, has concluded that *Cadomella* is 'a late member of the order Spiriferida'.

Our observations confirm the opinion of Cowen and Rudwick (1966) and Williams (1968) that *Cadomella* is a member of the Koninckinaea, a relationship hinted at by Muir-Wood in 1962.

In 1968 Williams was able only to use replicas for transmission electron-microscopy. Since then the use of the scanning electron microscope has greatly facilitated shell structural studies, in particular in allowing complete or fragmentary specimens to be searched for unusual or poorly known structures at a very wide range of magnifications. Furthermore, the process of replication may diminish or destroy remnants of primary shell on fossil species, a danger which is eliminated by direct study of the material under the scanning electron microscope.

SHELL STRUCTURE

The shell structures in all three species of *Cadomella* are the same, but differences occur in the absolute sizes and presumed duration of secretion of these structures, probably related to the much greater size of *C. davidsoni*. Details of the shell structure of *C. moorei* and *C. quenstedti* appear to be identical and here examples are figured only for the former species. The shell of *C. davidsoni* is considerably thicker than that of

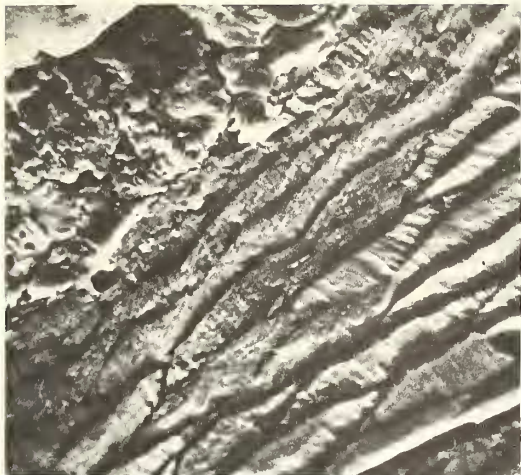
EXPLANATION OF PLATE 76

Specimens with B, BB, or ZB registration numbers are housed in the British Museum (Natural History), London.

Figs. 1-4. Scanning electron micrographs of the shell of *Cadomella davidsoni* (Eudes-Deslongchamps) from the Lias near Caen, Calvados, France. 1. Etched transverse section through primary (top left) and secondary shell layers. $\times 1050$, BB58575, from The Queen's University, Belfast (QUB) collections. 2. Fracture surface within the secondary layer, near the postero-median margin, showing the typical parallel stacking of fibres. Posterior to the top, viewed towards the exterior. $\times 450$, BB7242, from May, 8 km S. of Caen. 3. Transverse etched section through secondary and tertiary shell layers. $\times 500$, BB58575, from QUB collections. 4. Median longitudinal fracture surface, showing the junction of the secondary and tertiary layers. A temporary reversion to the development of fibres can be seen within the tertiary layer at the bottom left. $\times 525$, BB7242.

Figs. 5-6. Scanning electron micrographs of the shell of *Cadomella moorei* (Davidson) from the Upper Lias of Curey, about 20 km SSW. of Caen, Calvados, France. B14642. 5. Median longitudinal fracture surface through a ventral valve showing primary shell covering secondary layer fibres. Anterior is to the right and the different orientations of fibres can be seen. $\times 550$. 6. Fractured surface within the secondary layer showing the typical shape and stacking of standard fibres. $\times 1400$.

In all figures, except figure 2, the valve exteriors are to the top.



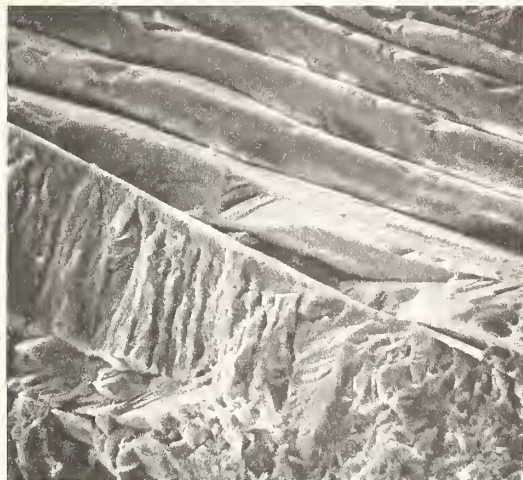
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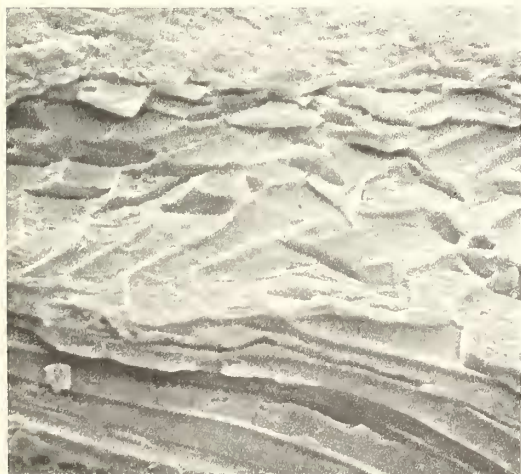
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C. moorei, to a large extent being composed of the tertiary shell layer. In *C. moorei* the primary layer is thin, apparently only a few μm thick (Pl. 76, fig. 5) while in *C. davidsouii* this layer reaches 20 μm thick (Pl. 76, fig. 1). Secondary fibres have a more or less parallel standard stacking and cross-sectional shape (Pl. 76, fig. 6). In *C. moorei* they measure 15–20 μm wide and about 4 μm thick (Pl. 76, figs. 5, 6) but measure up to 40 μm wide and 8 μm thick (Pl. 76, figs. 1–3), and appear more triangular in cross-section in *C. davidsouii*. During the ontogeny of *C. moorei* the first fibres grew tangentially to the valve margins, but within a few rows of the primary/secondary layer boundary they became reorientated to lie more or less radially (Pl. 76, fig. 5). A tertiary layer was secreted in which columnar prisms of calcite grew nearly perpendicularly inwards from the secondary fibres in both *C. moorei* and *C. davidsouii* (Pl. 76, figs. 3, 4). Within the much thicker tertiary layer of *C. davidsouii* sporadic reversion to the temporary secretion of fibres (Pl. 76, fig. 4) have been recognized and probably resulted from mantle regression close to the secondary/tertiary layer boundary.

The fact that *Cadomella* is reported to be pseudopunctate (Muir-Wood 1965, p. H438) has been used, in the past, as evidence of its strophomenide affinities. Williams (1968, p. 48) has recognized that the shell layers are inwardly deflected around rods of calcite which give rise to a tuberculate pattern on the internal surface of both valves. The rods, which measure up to 60 μm in diameter, exhibit a fine porous or granular texture (Pl. 77, fig. 1) so that they can even be recognized in sections through parts of the more massive-looking tertiary layer as well as the secondary layer. In most respects they resemble taleolae, the rod-like bodies which permeate the shells of many Strophomenida (e.g. Pl. 78, fig. 9), but equally justifiable is a comparison with the tubercles of *Megerlia*, a Recent terebratulide, the Jurassic thecideacean *Moorellia*, or the Triassic spire-bearing *Thecospira*, all of which exhibit a shell fabric bearing a likeness much closer to that of Spiriferida than any Strophomenida. Unlike *Moorellia* (Baker 1970, p. 87) but as in *Megerlia* and *Thecospira*, the tubercle cores are not continuous with material of the primary layer but appear to arise from clusters of fairly small secondary layer fibres which must have lain, initially, only a short distance from the primary/secondary layer boundary. Only those tubercles of *Cadomella* situated close to the valve margins appear to have been functional, for those rods located further from the shell edge (and hence secreted at an earlier stage in growth) appear to be overlapped by later secondary layer fibres. This situation is reminiscent of that in *Megerlia* where tubercles forming conspicuous outgrowths at the valve margins (Pl. 77, fig. 2) are, on occupying a position increasingly distant from the expanding shell edge, reduced to flattened scars (Pl. 77, fig. 3) by the processes of resorption and overgrowth of new shell material. Around such scars fibres are still deflected until finally they are submerged below a stream of secondary layer fibres whose ragged outlines are the only indication of any disruption of the underlying shell succession (Pl. 77, fig. 4).

At present it is uncertain what advantages were to be gained from having tuberculate shell margins, although an examination of the outer epithelial cells overlying tubercles in living *Megerlia* should give the answer. Provisionally it is noteworthy that well-developed tubercles in *Megerlia* are built up of a central complex of irregular calcite shreds which give way peripherally to more conventional secondary layer fibres (Pl. 77, fig. 5). Around the base of each tubercle well-developed fibres with smooth terminal faces are deflected on both sides; but near its flattened head the regular outlines break

down in a manner similar to that affecting fibres located on the periphery of muscle scars (Pl. 77, fig. 6) so that it is possible that the overlying outer epithelial cells were internally supported by dense concentrations of tonofibrils and served as attachment areas for some specialized component(s) of the mantle. On the other hand, as tubercles are only upstanding around the periphery of both valves, and are very rapidly resorbed and overlapped posteriorly, it is possible that these unusual outgrowths may have functioned as nothing more than a skeletal support for a fleshy protective grille.

DISCUSSION AND CONCLUSIONS

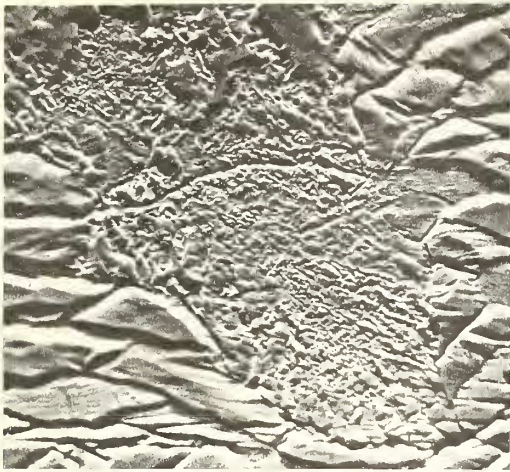
From studies of Recent brachiopods it is known that secretion of the shell is controlled by the outer mantle epithelium and, therefore, intimately bound up with the biochemistry of the animal. Thus it seems logical to assume a high level of systematic importance for shell structure. Work in progress (D. I. MacKinnon) shows that the shell structure of *Thecospira* and several koninckinacean genera is essentially spiriferide in nature, i.e. standard primary and fibrous secondary layers, with or without the addition of a tertiary prismatic layer internally. Observations recorded above show that *Cadomella* has an

EXPLANATION OF PLATE 77

- Fig. 1. Scanning electron micrograph of the shell of *Cadomella davidsoni* (Eudes-Deslongchamps) from the Lias of Curey, near Caen, France. BB58575, from QUB collections. Etched section through a tubercle submerged within the secondary layer of a brachial valve, $\times 525$.
- Figs. 2-6. Scanning electron micrographs of the shell of *Megerlia truncata* (Linnaeus); Recent. Mediterranean Sea. ZB3318, from QUB collections. 2. View of a tubercle located close to the valve margin showing the disposition of secondary fibres around its base and wall, and the breakdown of the mosaic when traced towards the porous core (see fig. 6). $\times 425$. 3. View of a tubercle submerged within secondary fibres and appearing as a flattened scar. $\times 525$. 4. View of the secondary layer internal mosaic modified where the fibres are overlapping a submerged tubercle. $\times 525$. 5. Etched section through part of a tubercle (top right) showing the inward deflection of secondary layer fibres. Valve interior to the left. $\times 1015$. ZB3319. 6. View of the tip surface of a tubercle showing the central region of irregular calcite shreds. $\times 825$.

EXPLANATION OF PLATE 78

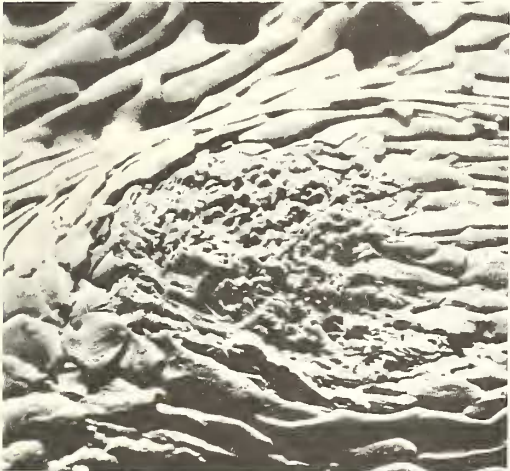
- Figs. 1-7 illustrate the umbonal regions of a variety of Spiriferida showing apical pedicle foramina.
- Fig. 1. Dorsal view of *Ampliolina amoena* Bittner (Koninckinidae) from the Triassic St. Cassian Beds near Cortina, Italy. $\times 4.4$. BB58567.
- Fig. 2. Dorsal view of *Cadomella davidsoni* (Eudes-Deslongchamps) (Cadomellacea) from the Upper Lias of May, Calvados, France. $\times 7$. BB58568.
- Figs. 3, 4. Dorsal views of two specimens of *Koninckella triassina* Bittner (Koninckinacea) from the Triassic St. Cassian Beds near Corvara, Italy. $\times 8$. BB58565-58566.
- Fig. 5. Dorsal view of *Homoeospira evax* (Hall) (Retziacea) from the Upper Silurian of Indiana, U.S.A. $\times 4.2$. B5355, Davidson Collection.
- Fig. 6. Dorsal view of the umbonal region of *Athyris vittata* Hall (Athyridacea) from the Mid Devonian of Ontario, Canada. $\times 6.3$. B7796, Davidson Collection.
- Fig. 7. Dorsal view of the umbonal region of *Tetractinella trigonella* (Schlotheim) (Athyridacea) from the Trias of Italy. $\times 5.5$. B7801, Davidson Collection.
- Figs. 8, 9. Scanning electron micrographs of the shell of a dorsal valve of a Permian chonetacean, *Dyoros* sp., from Russia, B2149. 8. Deeply exfoliated external view showing laminar sheets composed of calcitic blades. Anterior to the bottom. $\times 2400$. 9. Exfoliated internal surface, close to the antero-lateral margin (to bottom) showing shell lamellae deflected around the taleola of a pseudo-punctum, $\times 1150$.



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